# Exact and limit distributions of the largest fitness on correlated fitness landscapes

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We study the distribution of the maximum of a set of random fitnesses with fixed number of mutations in a model of biological evolution. The fitness variables are not independent and the correlations can be varied via a parameter $\ell = 1, ..., L$. We present analytical calculations for the following three solvable cases: (i) one-step mutants with arbitrary $\ell$ (ii) weakly correlated fitnesses with $\ell = L/2$ (iii) strongly correlated fitnesses with $\ell = 2$. In all these cases, we find that the limit distribution for the maximum fitness is not of the standard Gumbel form.



*Introduction*: Extreme value theory [1, 2] has found applications in various diverse fields ranging from physics of disordered systems such as spin glasses [3] and driven diffusive systems [4] to hydrology [5] and finance [6]. Here we are interested in its role in a model that describes the biological evolution of an infinitely large population of asexually replicating genetic sequences. The (logarithmic) population of a sequence increases linearly with time with the slope given by the sequence fitness and the intercept by the number $D = 0, ..., L$ of mutations with respect to the reference sequence [7]. It has been shown that out of the $S_D = \binom{L}{D}$ sequences present at constant $D$, the population dynamics involve only the sequence with the *largest fitness* at given $D$ [8].

If the sequence fitnesses are uncorrelated random variables chosen from a distribution decaying faster than a power law, the largest fitness is distributed according to the well known Gumbel distribution [1]. However as several experimental and theoretical studies have indicated that the realistic fitness landscapes are not completely random [9], we are led to study the extreme statistics of *correlated* fitnesses. In recent studies of extreme statistics of strongly correlated variables, deviations from the Gumbel distribution have been shown numerically (see, for example, [10]) or by analysing the tails of the extremal distribution [11, 12] but very few analytical results for the *full distribution* have been obtained [13, 14]. In this Letter, we obtain analytical results for the full distribution for both weak and strong correlations and show that it has a non-Gumbel form.

*Block model*: We consider a block model [15] of protein evolution in which a protein sequence of length $L$ is represented by a binary string of 0's and 1's and divided into $B$ blocks of equal length $\ell = L/B$. The block fitness $f_j(d)$ gives the fitness of a block with $d$ ones and the $j$th permutation of such $s_d = \binom{\ell}{d}$ possible random variables, each of which are chosen independently from a common exponential distribution. The sequence fitness is given by the average of the corresponding block fitnesses and two sequence fitnesses are correlated when they share at least one block fitness. An attractive feature of the block model is that the correlations amongst the fitnesses and the structure of the fitness landscape can be *tuned* with the block length $\ell$. For $\ell = 1$, the sequence fitnesses are strongly correlated and the fitness landscape is smooth, while for $\ell = L$, the model has uncorrelated fitnesses and the fitness landscape is maximally rugged. In the following, we work with even $L$ and consider $D \leq L/2$ as the results for $D > L/2$ can be obtained on simply replacing $D$ by $L - D$. The number $D$ of mutations is measured with respect to the reference sequence $\{0, 0, ...0\}$.

*One-step mutants, any $\ell$*: We first consider the extremal distribution for the fitnesses which carry only one mutation as this case can be solved for any $\ell$. Although there are $L$ one-step mutants, the number of sequences with distinct fitness is $\ell$ as the fitness $w_j$ of one-mutant neighbor is given by

$$w_j = \frac{(B-1)f_1(0) + f_j(1)}{B} \ , \ j = 1, ..., \ell \tag{1}$$

Since the cumulative distribution $\mathcal{P}_\ell(w, D, L)$ gives the probability that all the $w_j$'s are smaller than $w$, we have

$$\mathcal{P}_\ell(w, 1, L) = \int_0^\infty df_1(0) e^{-f_1(0)} \prod_{j=1}^{\ell} \int_0^\infty df_j(1) e^{-f_j(1)} \Theta(w - w_j) = \int_0^{\frac{Bw}{B-1}} df e^{-f} \left[1 - e^{-Bw} e^{(B-1)f}\right]^\ell \tag{2}$$

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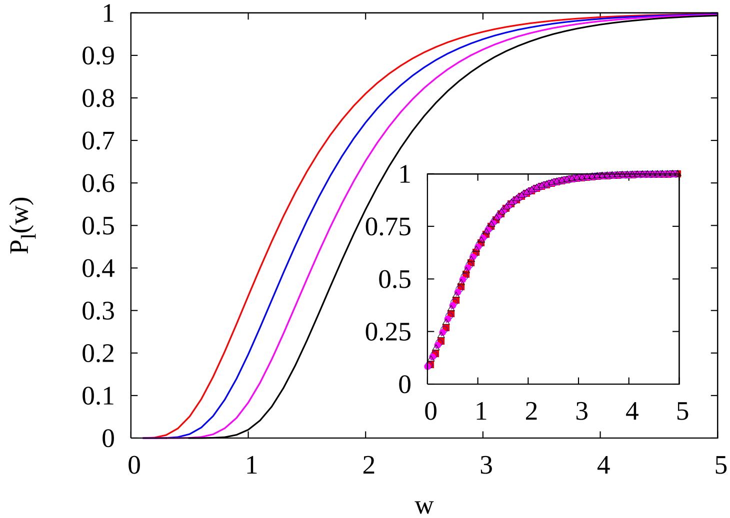


FIG. 1: Cumulative distribution $\mathcal{P}_l(w)$ for one-step mutants shown for $B = 3$ and $\ell = 5, 10, 20, 40$ (left to right) calculated using (2). The inset shows the data collapse when the distribution is plotted as a function of $u = w - B^{-1} \ln l$.

where $\Theta(..)$ is the Heaviside theta function. The cumulative distribution calculated using the above equation is shown in Fig. 1 for various $\ell$. For $\ell = 1$, the distribution $\mathcal{P}_1(w) = 1 + (L-2)^{-1}\left[e^{-Lw} - (L-1)e^{-Lw/(L-1)}\right]$ while the double exponential form $e^{-Le^{-w}}$ is obtained for $\ell = L$. Thus we have an example of a family of extremal distributions that interpolates between exponential and Gumbel distributions as correlations are varied.

The integral on the right hand side (RHS) of (2) does not seem to be exactly doable but for fixed $B$, it is possible to cast it in a scaling form which turns out to be of non-Gumbel form. Following an integration by parts, (2) can be rewritten as

$$\mathcal{P}_\ell(w,B) = (1-e^{-Bw})^\ell - \ell e^{-\frac{Bw}{B-1}} \int_0^{1-e^{-Bw}} dz \; z^{\ell-1}(1-z)^{\frac{-1}{B-1}} \tag{3}$$

$$= (1-e^{-Bw})^\ell e^{-\frac{Bw}{B-1}} \sum_{n=0}^{\infty} \binom{\frac{2-B}{B-1}+n}{n} \frac{n}{\ell+n}(1-e^{-Bw})^n \;,\; B > 1 \tag{4}$$

It is evident from the last expression that in the limit $\ell, w \to \infty$ with $\ell e^{-Bw}$ finite, $\mathcal{P}_\ell(w,B)$ deviates from Gumbel distribution for $B > 1$. Since the summand in (4) peaks around $n \sim e^{Bw} \gg 1$ as $w \to \infty$, the binomial coefficient can be approximated by $n^{\frac{2-B}{B-1}}/\Gamma(\frac{1}{B-1})$ for large $n$. Replacing the sum in (4) by an integral and defining the scaling variable $u = w - B^{-1}\ln \ell$ , we finally have

$$\mathcal{P}_\ell(w,B) \approx \frac{e^{-\ell e^{-Bw}}}{\Gamma(\frac{1}{B-1})} \int_0^\infty dn \; \frac{n^{\frac{1}{B-1}} e^{-n}}{\ell e^{-Bw}+n} = \frac{e^{\frac{-Bu}{B-1}}}{B-1}\Gamma\left(\frac{1}{1-B}, e^{-Bu}\right) \tag{5}$$

where the last expression holds for all $u$ except $u \to \infty$ and $\Gamma(a,x)$ is the incomplete gamma function [16]. Thus the limit distribution $\mathcal{P}_\ell(w,B)$ is a function of $u$ (see inset) and is of *traveling wave* form $F_B(w - vt)$ if we identify $t$ by $\ln \ell$ and velocity $v$ by $B^{-1}$ (also see (13) below). Note that unlike previous works [12, 14] that assume the distribution to be of traveling wave form, here we have shown the existence of such a solution.

*Block length $\ell = L/2$, any $D$*: As $B$ is an integer, $L/2$ is the largest value of $\ell$ at which correlations are nonzero. We now turn to this case with weak correlations and show that the distribution is of non-Gumbel form for any $D$. For $B = 2$, the fitness of a sequence with $D$ ones can be obtained by averaging over the block fitnesses with $d'$ ones in the first block and $d'' = D - d'$ ones in the second block. As there are $s_{d'}$ possible fitnesses for the first block and $s_{d''}$ for the second, the sequence fitness takes the following form:

$$w_{j,k}(d') = \frac{f_j(d') + f_k(d'')}{2} \;,\; d' = 0, ..., d_u \;,\; j = 1, ..., s_{d'} \;,\; k = 1, ..., s_{d''} \tag{6}$$

where $d_u = (D-1)/2$ for odd $D$ and $D/2$ for even $D$. The above equation gives distinct $w_{j,k}(d')$ for all $d'$ except $d' = D/2$ for which as $d' = d''$, distinct fitnesses are obtained when the index $k$ runs from $j$ to $s_{D/2}$. Thus the number

of distinct random variables are given by $(1/2)\left(\binom{2\ell}{D}+\binom{\ell}{D/2}(1-D \bmod 2)\right)$ [16] which increases as $\sim \ell^D$. As we shall see below, the extreme value distribution depends on whether $D$ is odd or even.
(i) For odd $D$, the fitnesses $w_{j,k}(d')$ are identically distributed as is evident from (6). The probability that all the fitnesses are smaller than $w$ is given by

$$\mathcal{P}_{L/2}(w,L)=\prod_{d'=0}^{d_u}\prod_{j=1}^{s_{d'}}\prod_{k=1}^{s_{d''}}\int_0^\infty df_j(d')e^{-f_j(d')}\int_0^\infty df_k(d'')e^{-f_k(d'')}\Theta(w-w_{j,k}(d')) \tag{7}$$

In the above expression, the product $\prod_{j=1}^{s_{d'}}\Theta(w-w_{j,k}(d'))$ in the integral over $f_k(d'')$ requires that $f_k(d'')<2w-f_j(d')$ for all $j=1,...,s_{d'}$. It is however sufficient to satisfy $f_k(d'')<2w-f_J(d')$ where $f_J(d')=\max\{f_1(d'),...,f_{s_{d'}}(d')\}$. Furthermore, as $f_k(d'')$ is positive, $2w-f_j(d')$ must also be positive for all $j$ thus restricting the domain of integration over $f_j(d')$ to $2w$. Thus we can write

$$\int_0^\infty df_k(d'')e^{-f_k(d'')}\prod_{j=1}^{s_{d'}}\Theta(2w-f_j(d')-f_k(d''))=\sum_{J=1}^{s_{d'}}\Theta(2w-f_J(d'))\prod_{\substack{j=1\\ j\neq J}}^{s_{d'}}\Theta(f_J(d')-f_j(d'))(1-e^{-2w+f_J(d')}) \tag{8}$$

which is independent of $k$. As a result, the product over $k$ in (7) can be done using the basic properties of Heaviside theta function. This immediately gives

$$\begin{aligned}\mathcal{P}_{L/2}(w,L) &= \prod_{d'=0}^{d_u}\sum_{J=1}^{s_{d'}}\int_0^{2w} df_J(d')e^{-f_J(d')}(1-e^{-2w+f_J(d')})^{s_{d''}}\prod_{\substack{j=1\\ j\neq J}}^{s_{d'}}\int_0^{f_J(d')} df_j(d')e^{-f_j(d')} &(9)\\ &= \prod_{d'=0}^{d_u} s_{d'}\int_0^{2w} df\ e^{-f}(1-e^{-2w+f})^{s_{d''}}(1-e^{-f})^{s_{d'}-1} &(10)\end{aligned}$$

For $D=1$, the above expression reduces to (2) with $\ell=L/2$. Following the steps similar to those leading to (4), we rewrite the last equation as

$$\mathcal{P}_{L/2}(w,L) = \prod_{d'=0}^{d_u} s_{d'}s_{d''}(1-e^{-2w})^{s_{d'}+s_{d''}}\sum_{n=0}^\infty\frac{(1-e^{-2w})^n}{(n+s_{d'})(n+s_{d''})}\ \frac{(n+s_{d''})!(n+s_{d'})!}{n!(n+s_{d'}+s_{d''})!} \tag{11}$$

To find the limit distribution, we first note that the factor corresponding to $d'=0$ in (10) is of the form (2). On comparing, we infer the scaling variable for $d'=0$ term to be $s_D e^{-2w}\sim \ell^D e^{-2w}$ when $\ell,w\to\infty$. This suggests that for arbitrary $d'$, the product $s_{d'}s_{d''}e^{-2w}$ remains finite while $s_{d'}e^{-2w}, s_{d''}e^{-2w}\to 0$ for large $\ell$ and $w$. In these scaling limits, for large $n$, we can write

$$\frac{(n+s_{d''})!(n+s_{d'})!}{n!(n+s_{d'}+s_{d''})!}\approx\left(\frac{n+s_{d'}}{n+s_{d'}+s_{d''}}\right)^{s_{d'}}\approx e^{-s_{d'}s_{d''}/n}=\exp\left[-e^{-2u_{d'}}/ne^{-2w}\right] \tag{12}$$

where $u_{d'}=w-\ln(\sqrt{s_{d'}s_{d''}})$. Approximating the sum in (11) by an integral, we finally get

$$\mathcal{P}_{L/2}(w,L)\approx\prod_{d'=0}^{d_u}e^{-2u_{d'}}\int_0^\infty\frac{dn}{n^2}\ e^{-n}\ e^{-\frac{e^{-2u_{d'}}}{n}}=\prod_{d'=0}^{d_u}2e^{-u_{d'}}K_1(2e^{-u_{d'}}) \tag{13}$$

where $K_n(x)$ is the modified Bessel function of the second kind [16]. Interestingly, the above distribution for $D=1$ has the same form as the cumulative distribution for the minimum energy in a random energy model with logarithmically correlated potential [14]. However, for $D>1$, there does not appear to be a single scaling variable.
(ii) For even $D$, since the fitnesses $w_{j,j}(D/2), j=1,...,s_{D/2}$ have a different distribution than the rest, the fitnesses are not identically distributed in this case. Using the results obtained above for $d'<D/2$ and separating the contribution due to $d'=D/2$, we can write

$$\mathcal{P}_{L/2}(w,L)=\prod_{d'=0}^{d_u-1}s_{d'}\int_0^{2w}df\ e^{-f}(1-e^{-2w+f})^{s_{d''}}(1-e^{-f})^{s_{d'}-1}\times\prod_{j=1}^{s_{D/2}}\prod_{k=j}^{s_{D/2}}\int_0^\infty df_j(D/2)e^{-f_j(D/2)}\Theta(w-w_{j,k}(D/2)) \tag{14}$$

By applying the same procedure as for odd $D$, the integral over $f_j(D/2)$ can be evaluated to give $1 - e^{-w}$. Within the same scaling limits as for odd $D$, we finally obtain

$$\mathcal{P}_{L/2}(w,L) \approx e^{-e^{-u_{D/2}}} \prod_{d'=0}^{d_u-1} 2e^{-u_{d'}} K_1(2e^{-u_{d'}}) \tag{15}$$

*Block length $\ell = 2$, any $D$*: For $\ell = 2$, although the sequence fitnesses are not only strongly correlated but non-identically distributed as well, it is possible to solve for the extreme value distribution exactly. If $n_1$ and $n_2$ denote the number of blocks with fitness $f_1(1)$ and $f_2(1)$ respectively, the number of blocks $n_3$ with fitness $f_1(2)$ at a fixed $D$ is given by $(D - n_1 - n_2)/2$. Furthermore, as the total number of blocks equals $B$, there are $(L - D - n_1 - n_2)/2$ number of blocks with fitness $f_1(0)$. Thus the fitness $w_{n_1,n_2}$ of a sequence with $D$ mutations obtained by averaging over the block fitnesses is writeable as

$$w_{n_1,n_2} = \frac{(L - D - n_1 - n_2) f_1(0) + 2n_1 f_1(1) + 2n_2 f_2(1) + (D - n_1 - n_2) f_1(2)}{L} \tag{16}$$

The cumulative distribution $\mathcal{P}_2(w,L)$ is given by

$$\mathcal{P}_2(w,L) = \int_0^\infty ... \int_0^\infty df_1(0) df_1(1) df_2(1) df_1(2) e^{-f_1(0)-f_1(1)-f_2(1)-f_1(2)} \prod_{n_1,n_2=n_{1,l},n_{2,l}}^{n_{1,u},n_{2,u}} \Theta(w - w_{n_1,n_2}) \tag{17}$$

where $n_{i,u}(n_{i,l})$ is the maximum(minimum) allowed value of $n_i, i = 1,2$ which, as discussed below, depends on whether $D$ is odd or even. Before proceeding further, we first note that in the product over theta functions in the above integrand, only those factors in which at least one of the indices $n_1, n_2$ are zero need to be retained and the rest are redundant. To see this, consider the theta functions with a given $n_1 + n_2$. Then if $f_1(1) > f_2(1)$, the fitness $w_{n_1,n_2} < w_{n_1+n_2,0}$ so that the condition $\Theta(w - w_{n_1,n_2})$ is automatically satisfied by $\Theta(w - w_{n_1+n_2,0})$. Similarly if $f_2(1) > f_1(1)$, it is enough to keep $\Theta(w - w_{0,n_1+n_2})$.

(i) For even $D$, as $n_3$ is an integer, both $n_1, n_2$ should be either odd or even which implies $n_{i,u} = D, n_{i,l} = 0$. Besides, the conditions $n_1 + n_2 \leq D, n_1 \leq D$ should be satisfied as $n_3$ is nonnegative. Counting the number of possibilities, we find that the total number of distinct fitnesses increases as $((D+2)/2)^2$ for $D \leq L/2$. Using the redundancy argument given above in (17), we have

$$\mathcal{P}_2(w,L) = \int_0^\infty \int_0^\infty df_1(0) df_1(2) e^{-f_1(0)-f_1(2)} \Theta(w - w_{0,0}) \left[ \int_0^\infty df_1(1) e^{-f_1(1)} \prod_{n_1=1}^{D} \Theta(w - w_{n_1,0}) \right]^2 \tag{18}$$

It is easy to see that the integral over $f_1(1)$ is nonzero provided $f_1(1) < \min\{\alpha + \beta, ..., (\alpha/D) + \beta\}$ where we have defined $\alpha = (Lw - (L-D) f_1(0) - D f_1(2))/2$ and $\beta = (f_1(0) + f_1(2))/2$. For $\alpha > 0$, this condition reduces to $f_1(1) < (\alpha/D) + \beta$ while for $\alpha < 0$, we require $f_1(1) < \alpha + \beta$. Thus we obtain

$$\int_0^\infty df_1(1) e^{-f_1(1)} \prod_{n_1=1}^{D} \Theta(w - w_{n_1,0}) = \Theta(\alpha) \Theta\left(\frac{\alpha}{D} + \beta\right) (1 - e^{-\frac{\alpha}{D} - \beta}) + \Theta(-\alpha) \Theta(\alpha + \beta)(1 - e^{-\alpha - \beta}) \tag{19}$$

Using $\Theta(w - w_{0,0}) = \Theta(\alpha)$, we finally get

$$\mathcal{P}_2(w,L) = \int_0^\infty \int_0^\infty df_1(0) df_1(2) e^{-f_1(0)-f_1(2)} \Theta(\alpha) (1 - e^{-\frac{\alpha}{D} - \beta})^2 = \int_0^{\frac{w}{1-y}} df e^{-f} (1 - e^{-\frac{w-(1-2y)f}{2y}})^2 (1 - e^{-\frac{w-(1-y)f}{y}}) \tag{20}$$

where $y = D/L$. The above integral can be easily computed and an explicit *exact expression* for the distribution $P_2(w,L) = d\mathcal{P}_2(w,L)/dw$ is given by

$$P_2(w,L) = \frac{-2e^{-\frac{w}{2y}}}{1-4y} + \frac{2e^{-\frac{3w}{2y}} - e^{-\frac{2w}{y}} + e^{-\frac{w}{(1-y)}}}{1-2y} + \frac{4ye^{-\frac{3w}{2(1-y)}}}{1-6y+8y^2} + \frac{y(e^{-\frac{w}{y}} - e^{-\frac{2w}{(1-y)}})}{1-5y+6y^2} \tag{21}$$

The mean $\bar{w}$ and the variance $\sigma^2$ calculated using $P_2(w)$ are then given by

$$\bar{w} = 1 + \frac{55}{36} y \ , \ \sigma^2 = 1 - \frac{3804}{1296} y + \frac{8135}{1296} y^2 \tag{22}$$

Thus the mean increases linearly with $y$ but the variance varies non-monotonically - it initially decreases with $y$ and then increases with the minimum at $y^* = 3804/16270 \approx 0.233$.
(ii) If $D$ is odd, we require that either $n_1$ is odd and $n_2$ is even or viceversa alongwith the condition $n_1+n_2 \leq D, n_1 \leq D$. In this case, $n_{i,u} = D, n_{i,l} = 1$ and we obtain $(D+1)(D+3)/4$ distinct fitnesses for $D \leq L/2$. Following the same reasoning as above, the cumulative distribution for odd $D$ can be written as

$$\mathcal{P}_2(w,L) = \int_0^\infty \int_0^\infty df_1(0) df_1(2) e^{-f_1(0)-f_1(2)} \left[ \int_0^\infty df_1(1) e^{-f_1(1)} \prod_{n_1=1}^{D} \Theta(w - w_{n_1,0}) \right]^2 \tag{23}$$

$$= \int_0^\infty \int_0^\infty df_1(0) df_1(2) e^{-f_1(0)-f_1(2)} \left[ \Theta(\alpha)\Theta\left(\frac{\alpha}{D}+\beta\right)(1-e^{-\frac{\alpha}{D}-\beta})^2 + \Theta(-\alpha)\Theta(\alpha+\beta)(1-e^{-\alpha-\beta})^2 \right] \tag{24}$$

The first term in the above sum reduces to (20). In the second term, the condition $\Theta(\alpha+\beta)$ requires that $0 < (D-1)f_1(2) < Lw - (L-D-1)f_1(0)$ and the condition $\Theta(-\alpha)$ can be satisfied if (i) $Df_1(2) > Lw-(L-D)f_1(0) > 0$ and (ii) $Df_1(2) > 0$ , $Lw - (L-D)f_1(0) < 0$. Putting all these conditions together, the second term can be evaluated. However for $L \gg 1$, the contribution of the second term to (24) can be neglected and we obtain the same result as for even $D$.

*Conclusions:* We have presented several analytical results for the extreme distribution in a model with tunable correlations. When the fitnesses are strongly correlated and non-identically distributed, full distribution is obtained exactly. For $D = 1$ and arbitrary $\ell$, we have shown that the limit distribution is of traveling wave form. As the limit distribution in the large $\ell$ limit for $D = 1$ and $\ell = L/2$ for any $D$ are seen to be of traveling wave form, we expect that this form survives for $\ell \sim \mathcal{O}(L)$ and any $D$. The weakly correlated model with $D = 1$ is found to obey the same extreme statistics as a random energy model with correlations. An elucidation of the connection between these two apparently unrelated models would be interesting.

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